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Large herbivore grazing limits small-mammal densities in Finnish Lapland

Michael den Herder[1,2], Samuli Helle[3], Pekka Niemelä[4], Heikki Henttonen[5] & Timo Helle[6]

[1)] *School of Forest Sciences, University of Eastern Finland, FI-80101 Joensuu, Finland*
[2)] *present address: European Forest Institute, Yliopistokatu 6, FI-80100 Joensuu, Finland (*corresponding author's e-mail: michael.denherder@efi.int)*
[3)] *Section of Ecology, Department of Biology, FI-20014 University of Turku, Finland*
[4)] *Section of Biodiversity and Environmental Science, Department of Biology, FI-20014 University of Turku, Finland*
[5)] *Natural Resources Institute Finland, Management and Production of Renewable Resources Unit, FI-01301 Vantaa, Finland*
[6)] *Natural Resources Institute Finland, Rovaniemi Research Unit, FI-96300 Rovaniemi, Finland*

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Grazing by large mammals can affect small-mammal populations by modifying the ground-layer vegetation, which provides them with food and shelter. The aim of this study was to investigate the impact of semi-domesticated reindeer grazing on small-mammal abundance in boreal forests/subarctic tundra ecosystems in a large-scale exclosure experiment in northernmost Finnish Lapland. In our experiment spanning four years, reindeer grazing affected the abundance of arvicoline voles, which were less abundant in grazed areas. This was probably due to a reduction in the abundance and height of bilberry, an important forage plant for both voles and reindeer. Changes in ground-layer vegetation affected the general condition of bank voles, which had significantly lower body mass in grazed areas. The abundance of insectivorous shrews was also reduced by grazing, probably due to a reduction in ground-dwelling invertebrates as an indirect effect of changes in the composition of ground-layer vegetation. A grazing-induced reduction in small mammal abundance can have far reaching ecological consequences for small-mammal population dynamics as well as mammalian and avian predators depending on small mammals as food.

Introduction

Large mammalian herbivores have not only been shown to directly affect vegetation composition and dynamics through biomass removal but also to change vegetation structure through physical disturbance. In northern Fennoscandia, severe browsing by moose (*Alces alces*) may prevent tree regeneration while browsing by semi-domesticated reindeer may affect the lower statured shrub and field layer (Angelstam *et al*. 2000, Suominen & Olofsson 2000, Olofsson *et al*. 2001, Ericsson *et al*. 2001). Heavy grazing by reindeer on ground layer vegetation may eventually eliminate the lichen carpet (Helle & Aspi 1983, Väre *et al.* 1995). In contrast to direct effects, indirect effects of large mammal herbivory are less frequently studied even though they may considerably affect ecosystems. By modifying the vegetation structure, large herbivores may indirectly affect small herbivores such as rodents (Steen *et al.* 2005, Ims *et al.* 2007) and their predators. Small rodents depend on the field layer vegetation that provides them with food and shelter against predators.

Small-rodent populations show strong fluctuations and temporarily rodents may occur at high densities. Causes for cyclic dynamics have been debated for decades. Even within a species, there are geographic differences in patterns in rodent dynamics (Hansson & Henttonen 1985, Hanski *et al.* 1991). For instance, the gradient in cycle length and amplitude in Finland suggests that the role of different predators also changes, i.e. predator community diversity declines towards the north (Hanski *et al.* 1991) where small mustelids are the dominant guild. It should be remembered, though, that many of the suggested mechanisms may apply only in limited regions. For example, Graham and Lambin (2002) showed that specialist mammalian predators are neither necessary nor sufficient to drive field vole (*Microtus agrestris*) population cycles in Scotland. A recent review by Prevedello *et al.* (2013) supports the view that animal population density (especially that of small mammals) is constrained by both food supply and predators. The search for mechanisms underlying the fascinating cyclic dynamics of small rodent populations is continuing and the potential role large mammalian herbivores play in influencing these dynamics deserves more attention.

Pronounced rodent cycles have prevailed in northern Fennoscandia for decades. However, a change in cyclicity started to emerge first in the northern taiga in the early and mid-1980s (Henttonen *et al.* 1987), and then in birch forests at Kilpisjärvi in the early 1990s. Hereafter, the vole cycles gradually disappeared or became much less pronounced and continued at irregular intervals. The change in dynamics has also extended further south in Swedish boreal forest (Hörnfeldt 2004). Large-scale geographic synchrony in the dynamics apparently also broke down at the same time (Henttonen & Wallgren 2001, Hörnfeldt 2004). However, during the previous 5–10 years, cycles and large geographic synchrony had returned, and during the years 2010–2011 the greatest vole peak in 40–60 year of time series data from Lapland was seen, followed by the typical deep cyclic crash in all species in 2012 (H. Henttonen pers. obs.).

Climate change, forestry, forest fragmentation, changes in land use and consequent changes in predator populations have been proposed as possible explanations for the change in cyclicity (Henttonen 2000, Ims *et al.* 2008, Hörnfeldt 2004, Cornulier *et al.* 2013). Some recent local studies on the impact of climate change on vole populations showed that the vole cycles have returned to southern Finland after a period of non-cyclic dynamics despite ongoing rapid climate change and milder winters (Brommer *et al.* 2010). Changing winter conditions have normally been related to the disappearance of cycles, but recently Korpela *et al.* (2013), using long-term data sets of vole fluctuations all over Finland, concluded that changes in the summer climate have been the most important feature. Nevertheless, it remains unclear to what extent vole populations are influenced by human-induced habitat changes such as forestry and other changes in land use. Steen *et al.* (2005) found that sheep grazing in Norway reduced the abundance of the field vole. The abundance of bank voles, whose diet differs from that of sheep, was not affected by sheep grazing. A study by Hörnfeldt (2004) considered reindeer grazing as an explanation for the change in small rodent cycles in northern Fennoscandia. Some studies reported that grazed plants increased the production of tripsin inhibitors, which can lead to retarded growth, a compressed breeding season, delayed sexual maturity, low recruitment, low survival and increased dispersal in lemming populations. For instance, Seldal *et al.* (1994) suggested that a grazing-induced increase in the production of trypsin inhibitors in food plants is a possible cause for the cyclic dynamics in small mammal populations. Other studies did not confirm that there is evidence for a grazing-induced defence consisting of trypsin inhibitors but did find grazing-induced variation in the amount of soluble plant proteins, which also may have consequences for herbivores (Lindgren *et al*. 2007). However, Ims *et al*. (2007) found that voles and lemmings were not negatively affected by reindeer grazing in tundra habitats. On the contrary, they observed a positive relationship between reindeer and small mammals. Nevertheless, studies demonstrating the effect of reindeer grazing on the abundance of small mammals are rare. Even if we consider a wider range of ecosystems, studies on the effects of large mammals on small-mammal populations are scarce and were carried out in tropical grasslands, desert scrublands, temperate forests and high elevation riparian habitats (Putman *et al*. 1989, Hazebroek *et al* 1995, Keesing 1998, Smit *et al*. 2001, Parsons *et al*. 2013).

The ecological impacts of herbivory by semi-domesticated reindeer can be numerous. The direct effects of reindeer on shrubs, dwarf shrubs, herbs, grasses and lichens have been documented in many studies (den Herder & Niemelä 2003, den Herder *et al*. 2003, 2004, 2008). There is also evidence that high reindeer densities can indirectly affect the species composition and abundance of herbivorous and ground-dwelling invertebrates (Suominen *et al*. 2003). This, in turn, may affect the abundance of insectivorous mammals such as shrews (*Sorex* spp.). Changes in ground-layer vegetation and food abundance is seen in the general condition of small-sized herbivores as a change in body mass (Ims *et al*. 2007). Studies in boreal forest or subarctic tundra ecosystems involving competitive interactions between differently sized herbivores are scarce. Possible impacts of large herbivores on small mammals have become especially interesting since contemporary Fennoscandian ecosystems experience high densities of semi-domesticated reindeer (Jernsletten & Klokov 2002). Therefore, it would be important to gain more evidence from a broader range of habitats and environmental conditions.

The effects of reindeer on small mammals were studied near Pallasjärvi, a lake in Finnish Lapland, during a period of four years (2004–2007) by monitoring vole densities inside and outside large-scale exclosures protecting the vegetation from grazing by reindeer. The main questions addressed in this research were: (1) Does grazing by reindeer have an effect on the abundance of small mammals? (2) Can these possible effects of reindeer grazing be seen in the condition of small mammals, e.g. body mass? (3) Does reindeer grazing affect the abundance and height of bilberry (*Vaccinium myrtillus*), an important resource providing both food and shelter for voles?

Material and methods

Study area

The study area was located on the west bank of Pallasjärvi (68°03´N, 24°09´E), a lake in Pallas-Ylläs National Park in northwestern Finnish Lapland. The area is characterised by relatively high fells, forests on slopes and mires/bogs in the valleys and belongs to the northern boreal vegetation zone (Ahti *et al*. 1968). The forest is predominantly old *Myrtillus*-type spruce forest mixed with birch, Scots pine and aspen. A more detailed description of the study site is given in Henttonen *et al*. (1987), and more information on rodent communities and population dynamics in Finnish Lapland can be found in Henttonen and Hanski (2000), Henttonen and Wallgren (2001), Hanski and Henttonen (2002). The study area was located in the area of the Kyrö herding association. In recent years, the gross density of semi-domesticated reindeer was 2 indiv. km^{-2}. The northern half of the area is used in winter and the southern half, where the study area was located, from early spring to late autumn (Helle 1982). In early summer, when the new leaves and shoots of bilberry are highly preferred by semi-domesticated reindeer (Skjenneberg & Slagsvold 1979), the reindeer density in the study area and its surroundings can considerably exceed the summer gross density (about 4 indiv. km^{-2}).

Experimental design

The effects of reindeer on small mammals were studied by using existing large-scale exclosures, protecting the vegetation from grazing by reindeer during 2004–2007. The fences would also exclude moose, which are less common in the area but can occasionally pass by. In 1988, three exclosures measuring 134 × 134 m (1.8 ha) were established on the west bank of Pallasjärvi. The exclosures were constructed of wooden poles and commercially available reindeer fence, which prevents access by reindeer but small mammals (voles, shrews and mustelids), hares and foxes are able to move in and out of the exclosures. Distances between the exclosures were about 700–2000 m. Each exclosure had a respective control area of the same size where reindeer were able to roam freely. Control areas were situated at a distance of about 100–500 m from the fenced exclosures. We thus had six study sites that were sampled for four consecutive years.

Trapping of small mammals

Small mammals were captured twice a year from 2004 to 2007. Each year, the first trapping session took place in early spring after snowmelt (beginning of June) and the second one at the end of summer (late August). In the centre of each exclosure or open control area, 36 live traps were placed in a 6 × 6 grid with 10 m between them. Traps were checked twice a day and trapping continued for three nights. Comparisons of small mammal densities between grazed control areas and ungrazed exclosures were based on the number of individuals caught per trapping session. Small mammals were captured with live traps (Ugglan model 2, Grahnab AB, Hillerstorp, Sweden). Oat seeds were used as bait, as were potatoes as they have higher water content. For each animal, we recorded the species, sex, age ("juvenile", "sub-adult" (non-breeding that has delayed maturation), "adult of the summer" or "overwintered"), reproductive status and body mass (g). Captured animals were marked by cutting the nails so that recaptured individuals could be recognised.

Abundance and size of available forage plants

Since bilberry (*Vaccinium myrtillus*) was the predominant dwarf shrub in the shrub layer in all grazed and ungrazed areas and as this plant is also an important forage plant for both voles (Selås *et al*. 2011) and semi-domesticated reindeer (Skjenneberg and Slagsvold 1979, Warenberg *et al*. 1997), we assessed its abundance to estimate food availability for voles. In addition, being the most abundant dwarf shrub in the study area, bilberry also has an important function in providing voles with shelters against predators. The abundance of bilberry was determined in summer 2005 by visually estimating the foliage projective cover of the plant in three 1 m^2 plots in the centre of each grazed and ungrazed area, with 20 m between plots. In each plot, the three tallest bilberry stems were measured to estimate the maximum height of the plant in grazed and ungrazed areas.

Statistical analysis

Differences in vole and shrew densities between grazed and ungrazed areas were analysed by pairwise comparisons using general linear mixed models, estimated by restricted maximum likelihood (REML) and the degrees of freedom, parameter estimates and standard errors of fixed effects calculated by the Kenward-Rogers method (Littell *et al*. 2006). Repeated sampling within study sites during the study period of four years were treated as repeated-measures assuming a 1st-order autoregressive covariance structure (Littell *et al*. 2006).

Only bank voles were used in the analysis of the effect of grazing on body mass, since this was the only species with sufficient data. This effect was examined using the same statistical model as above, but due to missing data on vole body mass from some study sites, it was not possible to fit the temporal covariance structure. Instead, study site was included as a random factor. In addition to treatment effects, this model included individual sex and age (subadult or adult) and year as well as their two-way interactions with treatment as fixed effects. Three-way interactions were not considered because very few individuals were captured at the beginning of the study period. Bilberry abundance and height were also analysed using general linear mixed models. In the case of abundance, study site was treated as a random factor whereas in the case of height the three samples per study site were also included as a random factor by nesting within study sites. All models assumed normally-distributed residuals as the marginal residuals of the models showed no patterns indicative of heteroskedastic variances and non-normality. All analyses were conducted with the SAS statistical software ver. 9.3 (SAS Institute Inc., Cary NC, USA).

Results

A total of 759 small mammals were captured during 5184 trap nights in the period 2004–2007. Bank vole (*Myodes glareolus*) (480 indiv.) was the most frequently captured species, followed by the grey-sided vole (*Myodes rufocanus*) (97 indiv.). Field voles (*Microtus agrestis*) (2 indiv.) were captured only sporadically. For the shrews, the common shrew (*Sorex araneus*) (111 indiv.) was the most frequently captured. Pygmy shrew (*Sorex minutus*) (47 indiv.), masked shrew (*Sorex caucutiens*) (20 indiv.) and least shrew (*Sorex minutissimus*) (1 indiv.) occurred in lower densities.

Our analysis shows that the effect of grazing on vole abundance depended on study year (Table 1) as indicated by a year × treatment interaction approaching significance ($F_{3,10.3} = 3.19$, $p = 0.07$). During the first three years, grazing had no effect on vole abundance ($F_{1,9.47} < 0.17$, $p > 0.69$), but during the year 2007 vole abundance was significantly lower in grazed study sites ($F_{1,9.47} = 12.42$, $p = 0.006$; Fig. 1a, Appendix 1a–c).

Grazing influenced shrew abundance as well, but this effect did not depend on study year (Table 1). Mean (± SE) shrew abundance for grazed and ungrazed areas was 8.63 (± 2.6) individuals and 13.75 (± 2.6) individuals per trapping season, respectively, and thus shrew densities were, on average 5.12 individuals per trapping season lower in the grazed than in the ungrazed areas (Fig. 1b, Appendix 1d–f).

There was a marginally significant difference in body mass of bank voles between grazed and ungrazed areas that seemed to depend on study year but not on sex or age (Table 2). Adjusted mean ± SE body mass of bank voles in grazed and ungrazed areas was 17.7 ± 0.38 g and 19.1 ± 0.36 g, respectively, but only in the last study year was this effect clearly statistically significant ($F_{1,5.7} = 9.75$, $p = 0.022$; Fig. 2). The adjusted mean body mass of bank voles also differed between adults (21.7 ± 0.32 g) and subadults (15.7 ± 0.31 g) and between females (18.7 ± 0.37 g) and males (18.3 ± 0.28 g).

Finally, our results showed that the abundance ($F_{1,4} = 9.77$, $p = 0.035$) and height ($F_{1,4} = 8.52$, $p = 0.043$) of bilberry were lower in the grazed than in the ungrazed areas (Fig. 3).

Table 1. The effects of reindeer grazing on the abundance of voles and shrews at Pallasjärvi.

	Est. ± SE	$df_{num, den}$	*F*	*p*
Voles				
Covariance parameters				
AR(1)	0.53 ± 0.27			
Residual	13.30 ± 6.11			
Fixed effects				
Treatment		1, 3.51	3.13	0.16
Year		3, 10.3	69.48	< 0.0001
Treatment × year		3, 10.3	3.19	0.07
Shrews				
Covariance parameters				
AR(1)	–0.30 ± 0.25			
Residual	2.73 ± 1.02			
Fixed effects				
Treatment		1, 9.6	9.74	0.011
Year		3, 11	3.79	0.044
Treatment × year		3, 11	0.03	0.99

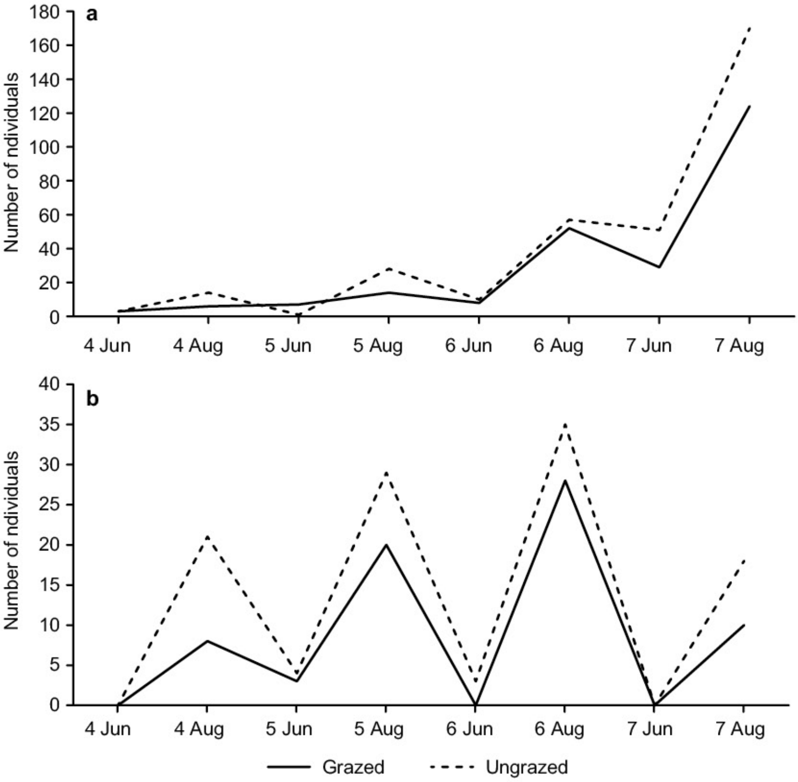

Fig. 1. Abundance (number of individuals) of (**a**) all voles and (**b**) shrews at Pallasjärvi in grazed and ungrazed areas.

Discussion

Our experimental study suggested that reindeer grazing had an impact on small mammal populations as both vole and shrew densities were lower in grazed areas. At the same time, reindeer feeding led to a reduction in ground-layer vegetation and height and abundance of bilberry was reduced by reindeer. Bilberry was the most abundant dwarf shrub in the study area providing shelter for voles. Moreover, it is an important forage plants for both voles and reindeer. Therefore, changes in ground-layer vegetation are likely to have at least some effect on vole populations. Effects of changes in ground-layer vegetation could be seen in the general condition of small mammals, as the mean body mass of bank voles in grazed areas was lower. The results

Table 2. Effect of reindeer grazing on body mass of bank voles.

	Est. ± SE	$df_{\text{num.den}}$	*F*	*p*
Covariance parameters				
Study site	0.24 ± 0.30			
Residual	7.84 ± 0.67			
Fixed effects				
Treatment		1, 11.6	4.11	0.066
Age		1, 274	339.2	< 0.0001
Sex		1, 275	13.62	0.0003
Year		3, 274	12.27	< 0.0001
Treatment × age		1, 274	1.76	0.57
Treatment × sex		1, 275	0.33	0.19
Treatment × year		3, 274	2.39	0.069

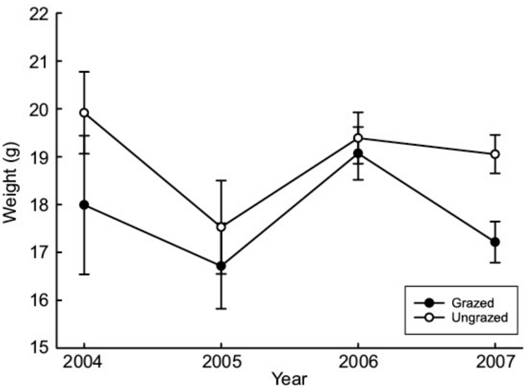

Fig. 2. Body mass of bank voles in grazed and ungrazed study sites. Error bars represent standard error of the means.

of this study provides evidence that by reducing ground layer vegetation and forage availability, reindeer grazing can limit small mammal densities. However, the study was too short to draw conclusions whether reindeer would have an effect on vole and shrew long-term dynamics. To see the effects on long-term dynamics we would need a study spanning at least a few population cycles. Nevertheless, this study is the first to demonstrate a possible negative impact of reindeer grazing on vole populations in northern boreal coniferous forest. In arctic willow thickets, Henden *et al*. (2011) did not find strong evidence for consistent impacts of browsing-induced changes of tundra shrubs on tundra voles. Contrary to that, Ims *et al*. (2007) found a strong positive relation between reindeer and small rodents. However, in temperate forests in England and the Netherlands, both population density and species richness of rodents were reduced by the presence of large herbivores (Putman *et al*. 1989, Hazebroek *et al*. 1995, Bush *et al*. 2012). In savannah habitats in Kenya, abundance of the pouched mouse *Saccostomus mearnsi* was reduced by grazing ungulates although there was no change in small mammal species diversity (Keesing 1998).

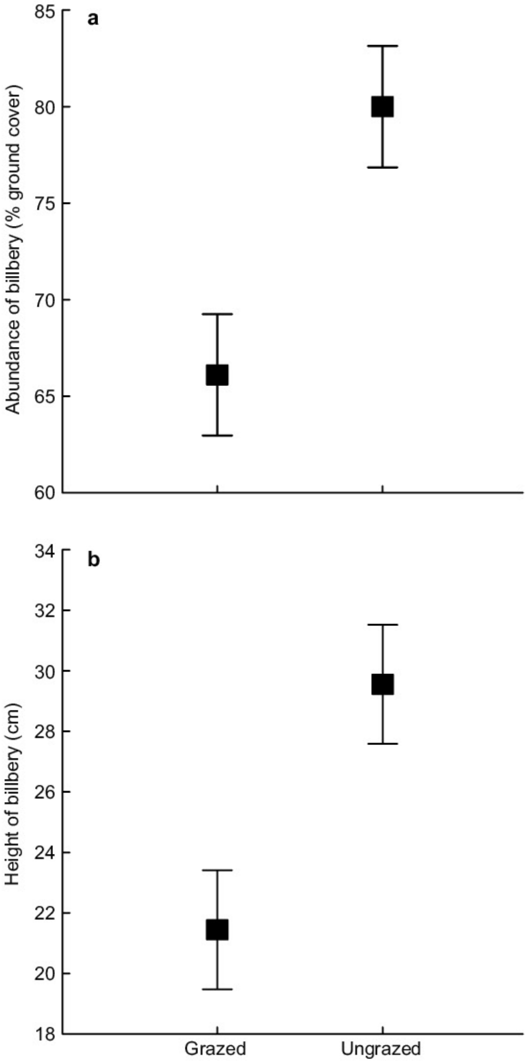

Fig. 3. (**a**) Abundance, and (**b**) height of bilberry in grazed and ungrazed areas in 2005. Error bars represent standard errors of the means.

Shrew densities were also reduced by reindeer grazing. A potential mechanism for this effect may have been a reduction in field- and shrub-layer vegetation, which, in turn, may have had a negative impact on the abundance of ground-dwelling invertebrates that shrews feed on. In previous studies, reindeer and moose in Sweden and Finland have been reported to have a negative impact on spider abundance but for other taxonomic groups of ground-dwelling invertebrates both positive and negative effects have been reported (Suominen 1999, Suominen *et al*. 1999, Suominen *et al*. 2003).

There are some potential mechanisms other than food availability that may partly explain our findings. It is likely that reindeer grazing creates more open habitats, making small mammals more vulnerable to mammalian and avian predators. This probably results in higher mortality in vole populations owing to higher predation pressure in the grazed areas as compared with that in the areas where reindeer grazing was prevented. This is in accordance with earlier experimental studies, which show that voles prefer sheltered habitats with a high ground vegetation layer, especially when high mustelid and avian predation risks are present (Korpimäki *et al*. 1996). Hence, both direct effects of predation, and/or avoidance of danger in open areas with a low bilberry layer, could contribute to higher population abundances of voles in more sheltered ungrazed areas. Accordingly, intra-specific competition for safe habitats within the vole population may increase as a result of intensive reindeer grazing on the bilberry layer. Dominant voles may occupy sheltered habitats at the expense of subdominant individuals, thus out-competing them in ungrazed areas. In accordance with this, both field data and aviary experiments have shown that larger field voles (*Microtus agrestis*) were more frequently found in good and sheltered habitats than in poor and vulnerable habitats (Koivunen *et al*. 1998). This is supported by our study as body mass of bank voles was higher in the ungrazed areas, which suggests that large and presumably dominant individuals may have had priority to sheltered habitats. Hence, dominant voles probably occupy ungrazed safe habitats more frequently than subdominant ones in the present study, which could have contributed to density differences of voles between the treatment and control sites.

Other potential mechanisms, in addition to predation, that may reduce vole population densities may be infanticidal behaviour (i.e. the killing and harassing of conspecific young). This especially concerns the bank vole, in which infanticide caused a 20% decrease in offspring survival, and even 25% loss in the production of recruits (Poikonen *et al*. 2008). Infanticidal behaviour emerges in vole populations quite easily, especially if food resources are limited (Tuomi *et al*. 1997), as in highly grazed areas. Hence, infanticidal behaviour could also be an explanation of decreased vole abundances in grazed areas, along with predation.

Bilberry (*Vaccinium myrtillus*) is a staple food plant for voles in winter and an important food plant in summer. Dense bilberry stands are also important as general microhabitats for voles. Any major decrease in the quantity of bilberry is thus likely to reduce survival through lack of winter food and shelter against predators. We suggest that increased bilberry densities in ungrazed areas apparently have potential to support higher population densities of voles and shrews. This is likely a result of the direct effects of bilberries as a resource providing food and shelter for voles, and indirectly by changes in insect abundance for shrews, and/or through the creation of more sheltered habitats against predators. Alternative explanations discussed in this study, however, may be of great importance as well and worthy of future experimental studies in order to explain the population dynamics of small mammals living in habitats under intensive grazing pressure.

As stated already in the introduction, the breakdown of rodent cycles in northern Fennoscandia, as well as its return, has puzzled scientist and so far the possible mechanism behind this phenomenon remains unknown. Our study was too short to draw any conclusions about possible impacts of reindeer on vole population cycles. Nevertheless, in our study, reindeer grazing had a small negative effect on vole densities. However, even if our exclosures were quite large, it would be impossible to predict if reindeer grazing would have a strong influence on vole population dynamics on a regional scale. Therefore, it is likely that some other factors are responsible for the disappearance of the vole cycles in northernmost Fennoscandia. Land use by forestry is relatively intense in northern Fennoscandia and has profound effects on landscape composition, e.g. by causing habitat loss and fragmentation through clearcutting. Disappearance of the grey-sided vole (*Myodes rufocanus*) from permanent sample plots in northern Sweden made the “Habitat fragmentation hypothesis” reasonable for at least partly explaining the decline in vole populations (Hörnfeldt 2004). Important habitats for the reproduction of grey-sided voles may have become so fragmented, that habitat patches in the landscape are no longer sufficiently large and common to permit building up vole densities to reach cyclic peaks. Henttonen (2000) and Henttonen and Wallgren (2001) have suggested that intensive forestry in the north has reduced the winter food supply (arboreal lichens in old forests) of *Myodes glareolus* and consequently its spring densities, thus indirectly affecting predation pressure on *Microtus*. Declining *Microtus* densities have affected the structure of predator communities and contributed to the disappearance of cycles.

In conclusion, our findings suggest that it is likely that reindeer grazing could decrease small mammal abundance by changing the quality and quantity of forage plants and modifying habitat structure. This could have far reaching consequences, not only for vegetation dynamics, but also on mammalian and avian predators which depend on small mammals as food.

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Appendix 1. Abundance (number of individuals) of (**a**–**c**, blocks 1–3, respectively) all microtine voles and (**d**–**f**, blocks 1–3, respectively) shrews at Pallasjärvi in grazed and ungrazed areas in three replicated blocks.